ENHANCING FARMLAND BIODIVERSITY THROUGH ENVIRONMENTAL FALLOWS: EFFECTS OF FALLOW TYPE AND LANDSCAPE

DOCTORAL THESIS

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ACADEMIC DISSERTATION

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CONTENTS

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This thesis is based on the following publications:

I Toivonen, M., Herzon, I. & Helenius, J. (2013) Environmental Fallows as a new policy tool to safeguard farmland biodiversity in Finland. Biological Conservation, 159, 355–366.

II Toivonen, M., Herzon, I. & Kuussaari, M. (2015) Differing effects of fallow type and landscape structure on the occurrence of plants, pollinators and birds on environmental fallows in Finland. Biological Conservation, 181, 36–43.

III Toivonen, M., Herzon, I. & Kuussaari, M. (2016) Community composition of butterflies and bumblebees in fallows: niche breadth and dispersal capacity modify responses to fallow type and landscape. Journal of Insect Conservation, 20, 23–34.

The publications are referred to in the text by their Roman numerals.

CONTRIBUTIONS

The contributions of the authors in the original articles of this thesis are presented in the following table.

	I	II	III
Planning the study	IH, MT, JH	MT, MK, IH	MT, MK, IH
Data collection	MT, IH	MT, IH	MT, IH
Data analyses	MT, IH	MT	MT
Manuscript preparation	MT, IH, JH	MT, IH, MK	MT, MK, IH

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ABSTRACT

Environmental fallows are fields that aim to produce environmental benefits instead of agricultural products. In many European countries, the establishment and management of fallows is funded via agri-environmental programmes. This thesis focuses on the biodiversity benefits of environmental fallows in boreal farmland. I examined the impacts of different fallow types and landscape structure on the diversity and species composition of multiple taxa in fallows. I also aimed to evaluate what fallow types, and in what landscape context, are needed to contribute to different biodiversity objectives: the promotion of conservation concern species, overall species diversity or ecosystem services.

In the first paper (I), I described vegetation types developed under the Finnish environmental fallow scheme based on an extensive survey of three agricultural regions. The studied fallow types included perennial types of meadow fallow and long-term grassland fallow, and annual types of game and landscape fields. The second (II) and third (III) papers were based on a quasi-experiment, where the occurrence of plants, butterflies, bumblebees and birds was studied in short-term meadow fallows and long-term grassland fallows located in four landscape types with varying forest and perennial grassland cover. First, I examined how the fallow and landscape types affected species richness and abundance in the four species groups (II). Next I focused on the species composition of butterflies and bumblebees (III). In particular, I studied the impacts of fallow type and landscape on species with narrow niches and low dispersal capacities, which are most vulnerable to environmental changes (III).

Species richness and composition of the studied species groups differed substantially between fallow types, and landscape context further modified the value of fallows. Meadow fallows established with low competitive meadow seed mixtures supported high plant species richness (I) and bumblebee abundance (II), reflecting good availability of floral resources. Grassland fallow vegetation varied substantially, but often resembled other farmland biotopes such as field margins or cultivated grasslands (I). In contrast, annual fallow types differed considerably from perennial fallows and other non-crop biotopes, thus enhancing landscape heterogeneity (I). High forest cover in the surrounding landscape increased plant species richness in perennial fallows (II). Long-term grassland fallows benefitted both butterflies in general (II), and butterflies and bumblebees with narrow niches and low dispersal capacities (III). The positive impacts were emphasized when long-term fallows were located in complex landscapes with high forest and perennial grassland cover (II, III). Birds used both short-term meadow fallows and long-term grassland fallows depending on the landscape context (II). The breeding density of open farmland birds was highest in short-term meadow fallows in landscapes rich in perennial grasslands (II). Foraging edge birds preferred short-term meadow fallows in

open landscapes and long-term grassland fallows in forested landscapes (II).

My results show that the biodiversity benefits of fallows can be enhanced by adapting fallows to the landscape context and to specific conservation objectives. If the objective is to support species of conservation concern, managing long-term fallows in complex landscapes rich in perennial grasslands is probably the best strategy. Overall biodiversity can also be enhanced in short-term fallows, especially if they are sown with diverse seed mixtures of species that are not too competitive in field conditions. Depending on the sown species, short-term fallows provide good possibilities to enhance landscape heterogeneity and promote ecosystem services. I also argue that defining landscape context on the grounds of the total coverage of semi-natural habitats is too simplistic when studying the landscape-moderated impacts of agri-environment schemes in boreal agricultural landscapes. Future studies should consider the specific roles of forest and perennial grasslands in driving the effectiveness of the schemes. In addition, the impacts of agri-environment schemes, including fallows, on realized ecosystem services should be investigated.

1 INTRODUCTION

1.1 COUNTERACTING BIODIVERSITY LOSS ON EUROPEAN FARMLAND

Agricultural intensification and concurrent abandonment of marginal land are the major threats to biodiversity on European farmland (Stoate et al. 2009). Biodiversity decline is related to the loss of ecological heterogeneity at multiple spatial and temporal scales, resulting from high-input farming practices, specialization in production lines and reduction of non-crop areas (Benton et al. 2003, Billeter et al. 2008, Kleijn et al. 2009). Extensively managed semi-natural grasslands harbour particularly high species richness of multiple species groups (Billeter et al. 2008, Hendrickx et al. 2007, Kivinen 2005, Pykälä 2000). These habitats have drastically declined over the last century through agricultural intensification and abandonment (Eriksson et al. 2002, Stoate et al. 2009).

Deleterious effects of agricultural intensification have been reported for several taxa, including plants (Baessler & Klotz 2006, Cousins et al. 2007, Hyvönen et al. 2003), invertebrates (Hendrickx et al. 2007, Potts et al. 2010) and birds (Donald et al. 2006, Guerrero et al. 2012). Besides its intrinsic value, biodiversity provides ecosystem services, such as pollination, pest control, decomposition and nutrient cycling, which are essential to human welfare. For instance, pollination by wild insects substantially contributes to global crop yields and human nutrition (Eilers et al. 2011, Garibaldi et al. 2013, Klein et al. 2007). Furthermore, ecosystem services reduce dependency on external inputs (Bommarco et al. 2013, Power 2010). Recent research has highlighted the need for ecological intensification in agriculture, which integrates the management of ecosystem services into crop production systems to increase yield levels and stability, while minimizing negative impacts on ecosystems (Bommarco et al. 2013, Deguines et al. 2014, Doré et al. 2011, Tittonell 2014).

Agri-environment schemes (AES) are the main tool for biodiversity conservation in agroecosystems in the European Union (EU). The schemes aim to enhance wildlife by restricting farming intensity, encouraging farmers to maintain low-input farming practices or promoting the maintenance and establishment of landscape elements such as wildflower strips, fallows and wetlands. Specific schemes are also targeted at providing resources for endangered species. However, despite the major public investments in AES, farmland biodiversity has continued to decline (Kleijn et al. 2011, Stoate et al. 2009, Whittingham 2011). Extensive research on AES during the last 15 years has revealed that the biodiversity effects of the schemes are mixed, and vary, for example, depending on the target species group, type of the measure, landscape context and guidance provided for farmers (Batáry et al. 2011, 2015, Concepción et al., 2012, Kleijn et al. 2011, Scheper et al. 2013, Whittingham 2011).

1.2 DESIGNING EFFECTIVE CONSERVATION MEASURES

In recent years, a growing body of literature has examined the key determinants concerning the effectiveness of biodiversity conservation measures on farmland. Several studies have pointed out that AES targeted at biodiversity should be adapted to the landscapes and farming systems of the regions where they are implemented (Batáry et al. 2011, Concepción et al. 2012, Kleijn et al. 2011, Scheper et al. 2013). According to the conceptual model of Kleijn et al. (2011), the biodiversity effects of conservation initiatives are a function of conservation-induced ecological contrast, land-use intensity and landscape context. Ecological contrast, created through reduction in land-use intensity, is the extent to which agri-environmental management improves resource availability for the target species relative to conventional management. Landscape context determines how species are able to respond to this ecological contrast. The impacts of AES on biodiversity are usually more pronounced in structurally simple landscapes (1–20% semi-natural habitat) than in cleared (<1% semi-natural habitat) or complex landscapes (>20% semi-natural habitat) (Batáry et al. 2011, Concepción et al. 2012, Kleijn et al. 2011, Tscharntke et al. 2005). The pattern results from the fact that cleared landscapes lack potential colonizers, whereas the impact of AES may not be recognizable in complex landscapes, because the colonization of wild species from semi-natural habitats allows for high diversity also in conventionally managed sites (Tscharntke et al. 2005).

So far, much of our understanding of the landscape-moderated impacts of AES is based on studies from Western and Central Europe. These areas differ substantially from boreal agricultural landscapes characterized by landscape mosaics of forest and fields. Although forest matrix have been reported to enhance the diversity of diurnal Lepidoptera and plants in grasslands (Kivinen et al. 2006, Kuussaari et al. 2007, Öckinger et al. 2012a, b), more information is still needed concerning the role of forests in moderating AES effectiveness. Furthermore, special characteristics of agricultural land-use in Northern Europe may modify the impacts of AES. For instance, crop production in Scandinavia is characterized by the production of spring-sown cereals, whereas autumn-sown cereals dominate in Western and Central Europe. The differences in cropping systems are likely to affect the extent of conservation-induced ecological contrast and its temporal variation.

Effective biodiversity conservation also requires clearly defined conservation objectives. Kleijn et al. (2011) distinguish two main types of objectives: conservation initiatives addressing the intrinsic value of biodiversity and those focusing on functional biodiversity. The former aim to conserve either all possible species, or declining or endangered species, whereas the latter promote species that provide specific ecosystem services such as crop pollination (Carvell et al. 2007, Wratten et al. 2012) or pest control (Fiedler et al. 2008, Ramsden et al. 2015). Although AES targeted at particular conservation objectives usually also provide secondary benefits for biodiversity, designing multi-purpose measures is rarely possible without trade-offs between different objectives (Bullock et al. 2011, Fiedler et al. 2008, Macfadyen et al. 2012, Wratten et al. 2012). In general, conservation efforts with intrinsic biodiversity objectives are most effective in complex landscapes where biodiversity is still high and rare species occur, whereas the largest benefits from the initiatives targeted at functional biodiversity can be expected in simple landscapes (Kleijn et al. 2011, Korpela et al. 2013, Tscharntke et al. 2005).

Furthermore, recent studies have emphasized the importance of suitable biodiversity indicators when assessing the impacts of conservation measures on farmland (Filippi-Codaccioni et al. 2010, Kleijn et al. 2011). The question has arisen whether studies focusing exclusively on species richness and abundance have given too optimistic messages concerning biodiversity status and fate (Filippi-Codaccioni et al. 2010). To draw reliable conclusions on AES impacts, attention should also be paid to community composition and species traits (Filippi-Codaccioni et al. 2010, Gámez-Virués et al. 2015). Consideration of community composition enables the detection of biotic homogenization, an important facet of biodiversity loss (Bühler & Roth 2011, Ekroos et al. 2010). Community composition at a particular site is shaped by environmental conditions that act as filters of species traits (Gámez-Virués et al. 2015, Marteinsdóttir & Eriksson 2014). To pass through these filters and join the community, species have to possess appropriate traits. Species traits can be used to predict species' contributions to ecosystem services and tolerance to environmental changes (Díaz et al. 2013, Filippi-Codaccioni et al. 2010). For example, while AES often promote common farmland species, they appear to be inefficient in protecting habitat specialists and poor dispersers that are most vulnerable to habitat loss and fragmentation (Ekroos et al. 2010, Haaland et al. 2010, Korpela et al. 2013). It is also noteworthy that local species enhancement through conservation measures is a poor indicator of population-level response, because ecological processes such as source-sink dynamics obscure the effect (Kleijn et al. 2011). However, so far few studies have related the impacts of AES to large-scale biodiversity trends (Kleijn et al. 2011).

1.3 FALLOWS IN BIODIVERSITY CONSERVATION

The introduction of fallow land in intensively-managed agricultural areas is a potential measure to enhance farmland biodiversity (Stoate et al. 2009, Van Buskirk & Willi 2004). Appropriately managed and sited fallows also deliver other environmental benefits such as a reduction in nutrient losses (Stoate et al. 2009), mitigation of greenhouse gas emissions (Smith et al. 2008) and landscape amenity (Odgaard et al. 2013). Temporarily setting a section of farmland aside of production has traditionally played an important role in rebuilding soil fertility and controlling pests and weeds. In the EU, compulsory set-asides were part of the Common Agricultural Policy (CAP) in 1992–2008. Originally intended to reduce production surpluses, set-asides became a tool for conserving farmland biodiversity (Van Buskirk &

Willi 2004). However, increases in agricultural commodity prices led to the abolition of the set-aside scheme in 2008.

The introduction and management of fallows is currently funded via voluntary AES in several European countries (Keenleyside et al. 2011, Scheper et al. 2013). Establishment methods and seed mixtures vary between the schemes. Fallows can be established on patches or strips of arable land through natural regeneration or by sowing. Seed mixtures usually contain grasses or wildflowers alone or in combination (Haaland et al. 2011, Keenleyside et al. 2011). Additionally, some fallows mostly contain legumes to promote pollinators or birds (Keenleyside et al. 2011, Pywell et al. 2011). Fallows can be rotational, i.e. in a different place every year, or long-term, retained in the same place for several years or even decades. The management of perennial fallows also varies, mowing being the most common management method.

As regards to the biodiversity impacts of fallows, the determinants of local habitat quality have been rather extensively studied. They include local environmental factors such as soil type and fertility (Boatman et al. 2011, Hansson & Fogelfors 1998), seed mixture (Alanen et al. 2011, Haaland et al. 2011, Kuussaari et al. 2011, Tscharntke et al. 2011), establishment and management methods (Boatman et al. 2011, Haaland et al. 2011, Tscharntke et al. 2011) and successional age of fallows (Alanen et al. 2011, Firbank et al. 2003, Frank et al. 2009, Hyvönen & Huusela-Veistola 2011, Tscharntke et al. 2011). Species responses to specific fallow features vary, but some general patterns have emerged: the species richness and population densities of relatively sedentary species groups, such as butterflies, moths and predatory arthropods, appear to increase with the successional age of the fallow (Alanen et al. 2011, Denys & Tscharntke 2002, Frank et al. 2009, Kuussaari et al. 2011). In contrast, bumblebees and birds can also be promoted through short-term fallows, assuming that food and nesting sites are available (Firbank et al. 2003, Henderson et al. 2000, Kuussaari et al. 2011, Steffan-Dewenter & Tscharntke 2001, Tscharntke et al. 2011). In short-term fallows, target organisms can be efficiently supported by sowing a seed mixture that provides specific plant resources such as nectar and pollen (Pywell et al. 2011, Ramsden et al. 2015).

So far, few studies have assessed how the biodiversity impacts of fallows are moderated by landscape context (but see Korpela et al. 2013). This issue is related to the question of how fallows differ from other farmland biotopes such as semi-natural grasslands. Information on the topic is scarce, although a few studies comparing plant and insect communities in fallows and perennial margins have indicated that the biotopes have complementary roles in supporting species or ecosystem functioning (Alanen et al. 2011, Ma & Herzon 2014). In addition to non-crop habitats, comparing the species communities of fallows with those of croplands, such as cultivated grasslands, could help in developing fallowing schemes that create large ecological contrasts, thus effectively enhancing landscape- and regional-level diversity.

Box 1. Environmental fallows in Finland

The Finnish AES of Environmental Fallows, introduced in 2009, was one of the first national biodiversity-targeted fallow schemes in the EU. Since its introduction, environmental fallows have covered 5–7% (118 200–162 800 ha) of Finnish agricultural land, which means that their potential impact on farmland biodiversity is considerable on the national scale. The scheme includes two main fallow types: long-term grassland fallows and biodiversity fields (Table 1). Along with promoting biodiversity, long-term grassland fallows aim to protect soil from erosion and nutrient leaching, improve soil structure and reduce pesticide use. Biodiversity fields are established for supporting wildlife and providing landscape amenity. They include sub-types of meadow fallow, game fields, landscape fields, and since 2015, bird fields. Each type is sown with specific seed mixtures designed to provide resources for pollinators, birds or game animals, or improve the landscape's visual appearance. Meadow and bird fields have perennial vegetation, whereas game and landscape fields are annual fallow types.

2 AIMS OF THE THESIS

The aim of this thesis is to examine the factors affecting biodiversity values of fallows on boreal farmland. The conceptual model of Kleijn et al. (2011) forms the theoretical framework for the thesis (Fig. 1). In particular, I focus on the impacts of different fallow types and landscape structure on the species diversity and community composition of plants, butterflies, bumblebees and birds. The studied species groups vary in functional traits, such as mobility and resource requirements, and are thus likely to respond differently to fallow types and landscape context. Specifically, I aim to answer the following three questions:

- How do different fallow types support the diversity of plants (I, II), butterflies (II, III), bumblebees (II, III) and birds (II) on boreal farmland? The studied fallow types include perennial types of long-term grassland fallow and short-term meadow fallow (I, II, III), and annual types of game and landscape fields (I).
- How does the surrounding landscape modify the benefits of fallows (II, III)? The studied landscape variables are the amount of forest and perennial grasslands.
- Does the conservation of rare species or species vulnerable to environmental changes require different fallow types and landscapes than the promotion of overall diversity (I, II, III)?

Based on the results, I discuss the effectiveness of different fallowing strategies for biodiversity conservation from the perspectives of different conservation objectives. I also evaluate the role of the current Finnish AES of environmental fallows for biodiversity conservation in Finland, and suggest improvements to the scheme.

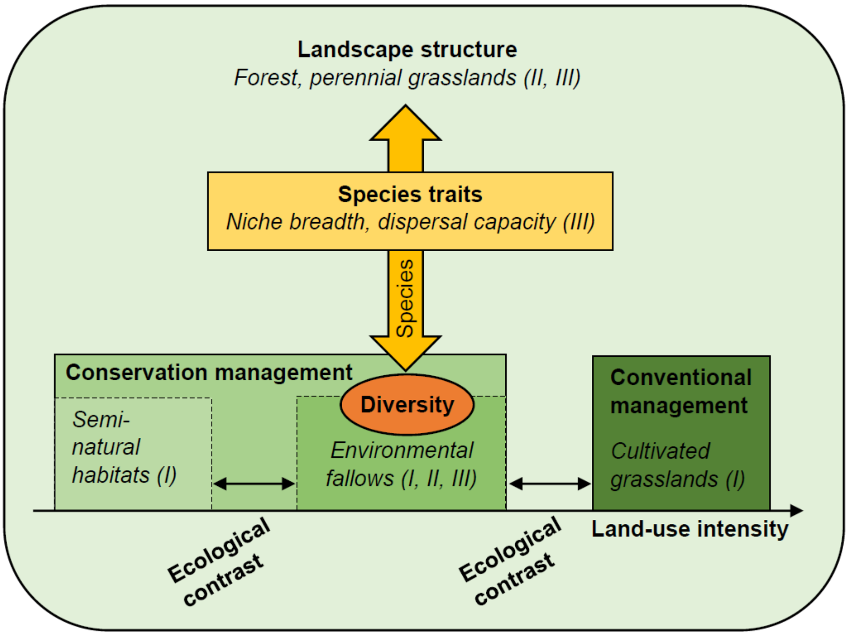

Figure 1 Biodiversity effects of conservation management on farmland depend on land-use intensity, landscape structure and conservation-induced ecological contrast in resource availability (Kleijn et al. 2011). Additionally, the responses of individual species to local management and landscape are determined by species traits (Gámez-Virués et al. 2015). This thesis focuses on the species diversity and community composition of multiple taxa in environmental fallows (papers I–III). The studied landscape factors are forest and perennial grassland covers (II, III), and the species traits are niche breadth and dispersal capacity (III). Fallow vegetation is compared to semi-natural habitats and cultivated grasslands to evaluate the ecological contrast between the biotope types (I).

3 MATERIALS AND METHODS

3.1 FALLOW TYPES

This study focuses on four fallow types that are included in the Finnish environmental fallow scheme: long-term grassland fallow, meadow fallow, game field and landscape field (Fig. 2). The main characteristics of the types are presented in Table 1.

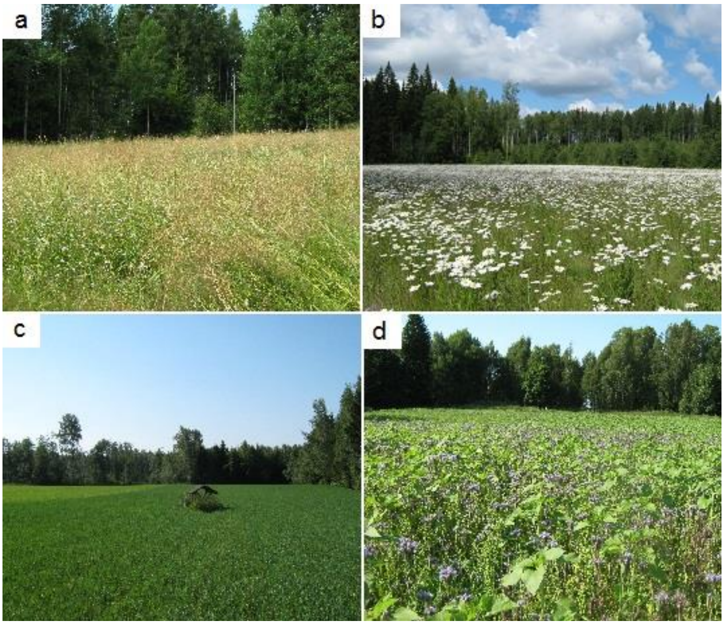

Figure 2 The studied fallow types are long-term grassland fallow (a), meadow fallow (b), game field (c) and landscape field (d).

Table 1 Major terms for environmental fallow subsidies in the studied fallow types in Finland.

	Long-term grassland fallow	Biodiversity fields		
		Meadow fallow	Game field	Landscape field
Seed mixture	Perennial grasses, max 20% legumes, or old grassland	Low competitive grasses (e.g. *Festuca ovina*), perennial meadow plants (e.g. *Leucanthemum vulgare, Campanula patula),* annual plants (e.g. *Centaurea cyanus*, *Phacelia tanacetifolia*)	Annual plants for game animals, at least two species (e.g. *Brassica rapa* ssp. *oleifera, Pisum sativum,* cereals*)*	Annual "landscape" plants, at least two species (e.g. *Helianthus annuus, Centaurea cyanus)*
Termination	At the earliest, autumn of 2nd year or summer (if followed by autumn crop)	At the earliest, autumn of 2nd year or summer (if followed by autumn crop)	Spring of 2nd year	Spring of 2nd year
Mowing	At least every 2nd year, at any time	Not compulsory, after 1.8.	Not compulsory, after 1.8.	Not compulsory, after 1.8.
Biomass use	Can be grazed, or biomass can be collected and utilized	Biomass can be collected and utilized	Only for wildlife	Biomass can be collected and utilized
Fertilization	Minimal fertilization at establishment allowed	Minimal fertilization at establishment allowed	Minimal fertilization at establishment allowed	Minimal fertilization at establishment allowed
Herbicides	Only at termination	No	No	No
Maximum area in a farm	Regions with low grassland cover: 20% of the field area; regions with high grassland cover: 5%	Biodiversity fields in total: 15% of the field area		
	All fallow types in total: 20% of the field area			

3.2 FIELD STUDIES

Data for the three papers (I–III) were collected in two separate field studies on environmental fallows. The vegetation survey (results reported in paper I) was performed in three regions of Finland during 2010–2011. The quasi-experiment studying the impacts of perennial fallow types and landscape structure on the occurrence of plants, butterflies, bumblebees and birds (results reported in papers II–III) was conducted in Southern Finland in 2013.

3.2.1 Vegetation survey

The vegetation survey was carried out in the Uusimaa, Pirkanmaa and Pohjois-Pohjanmaa regions (Fig. 3). Uusimaa, located on the south coast of Finland, is a cereal production region. Despite intensive agriculture, species richness in agricultural landscapes is nationally high due to advantageous climatic conditions (Kivinen et al. 2006). Pirkanmaa, in south-western Finland, is an animal husbandry region. Farm and field sizes are smaller and landscape structure more fine-grained than in the other regions. The northernmost region Pohjois-Pohjanmaa is also characterized by animal husbandry. In this region, agriculture is mainly concentrated on the coastal lowlands.

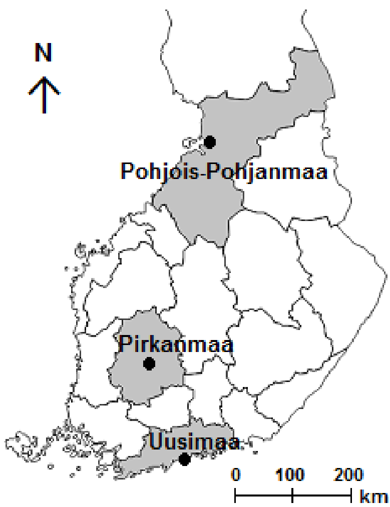

Figure 3 Location of the three study regions in Finland. Regional centres Helsinki (in Uusimaa), Tampere (Pirkanmaa) and Oulu (Pohjois-Pohjanmaa) are marked with dots. The figure contains data from the National Land Survey of Finland Municipal Division Database 01/2015.

Farms from each region were randomly selected from those situated within a 100-km distance of the regional centre (Fig. 3). A total of 229 fallows were selected according to the ratio 3:3:1:1, representing the four fallow types: long-term grassland fallow, meadow fallow, game field and landscape field. The higher proportion of perennial than annual fallows in the study was based on the assumption that the vegetation of the perennial fallow types would be more varying. Vegetation surveys were conducted in Uusimaa and Pohjois-Pohjanmaa in 2010, and in Pirkanmaa in 2011, between the end of June and mid-August. In addition, five randomly selected production grasslands were sampled in 2011 in the Uusimaa region.

In the vegetation survey, vegetation height and density, and the coverage of individual plant species and bare ground were measured on 12.5-m-long and 1-m-wide transects that were systematically placed within each fallow. The number of transects per fallow varied between one and four, depending on the area of the fallow (0–0.1 ha = 1 transect, 0.1–0.5 ha = 2 transects, 0.5–1 ha = 3 transects, ≥1 ha = 4 transects). The coverages of individual species were estimated using a 9-grade logarithmic scale (1 = 0–0.125%, 2 = 0.125–0.5%, 3 = 0.5–2%, 4 = 2–4%, 5 = 4–8%, 6 = 8–16%, 7 = 16–32%, 8 = 32–64%, 9 = 64–100%). Additionally, data on fallow age, yield level of the preceding crop and forest cover within a 1-km buffer around the fallow's central point were collected to understand the factors affecting fallow vegetation.

3.2.2 Quasi-experiment

The quasi-experiment focusing on the impacts of perennial fallow types and landscapes structure on the occurrence of plants, butterflies, bumblebees and birds was performed in 40 perennial fallows in Southern Finland. The study fields were located in the Uusimaa region (Fig. 3), apart from four plots that were situated within a 10-km distance north of Uusimaa's border. The experiment focused on two perennial fallow types: old grassland fallows (at least eight years old) and younger meadow fallows (three or four years old). Both were selected in four landscape types with different forest and perennial grassland cover (high forest and grassland cover, high forest and low grassland cover, low forest and high grassland cover, low forest and grassland cover). Forest and perennial grassland areas were calculated for a buffer with a 500-m radius around the central point of the fallow.

Data on all studied species groups were collected in the fallows during the summer of 2013. Butterflies and bumblebees were counted four times in 2-week intervals, from early June to late July, using the standard line transect method (Pollard & Yates 1993). The transects were 200 m long and divided into four 50-m-long sections. Plant data were collected in early July along two of the transect sections used in insect counting. The coverages of individual plant species, bare ground and litter were estimated in an area of 50 m * 1 m using the same logarithmic scale as in the vegetation survey. Farmland birds were counted applying a combination of the point and mapping methods (Bibby et al. 1992) with three visits from mid-May to late July. During the visit, birds were first observed from a vantage point for 10 min, after which the field was crossed at 100 m intervals. The counter recorded observations of territorial behaviour, foraging or other registrations, except those observed during flight, within the fallow and at its edges. For analyses, birds were divided into open farmland species, which both breed and forage on fields, and edge species, which forage on fields but nest in forest edges or trees and bushes along field margins.

3.3 SPECIES TRAITS

For butterflies and bumblebees, the impacts of fallow type and landscape structure were examined in respect to two species traits – niche breadth and dispersal capacity (III). These traits are thought to be key factors modifying the responses of flower-visiting insects to habitat loss and fragmentation (Bommarco et al. 2010, Öckinger et al. 2010, Warren et al. 2001). Trait data were compiled from the existing literature. Niche breadth was expressed as the adult habitat breadth of butterflies (Komonen et al. 2004) and the diet breadth of bumblebees as measured by tongue length (Bäckman & Tiainen 2002). The wing span of butterflies (Kuussaari et al. 2014, Marttila et al. 1990) and body size of bumblebees as measured by inter-tegular distance (Bommarco et al. 2010, Greenleaf et al. 2007) were used as proxies of dispersal capacity.

3.4 STATISTICAL ANALYSES

3.4.1 Linear models

The characteristics of fallows and the surrounding landscape modifying the species richness, abundance and trait composition of the studied species groups were examined using general linear models (I), general linear mixed models (I) and generalized least squares models (II, III). The response variables were plant species richness (I, II), the species richness and abundance of bumblebees, butterflies and birds (II), and the mean niche breadth and dispersal capacity of butterfly and bumblebee species and individuals (III).

General linear models with the hypothesis testing approach were used to examine the factors affecting plant species richness in fallows in paper I. The species richness of all study plots was modelled in respect to the region, fallow type and their interaction. In addition, the species richness of perennial fallows was modelled separately using region, fallow type and the following covariates as explanatory variables: field size, age of fallow, vegetation structure, variations in height and density, and forest cover in the surrounding landscape. To clarify the impact of field size on vegetation diversity, the same models were also run using transects as a sample unit and plots as a random factor in the general linear mixed model.

The information theoretic approach was applied in papers II and III to identify the contributions of fallow types, and forest and grassland cover in the surrounding landscape to the species richness of plants, butterflies, bumblebees and birds (II), and the mean niche breadth and dispersal capacity of butterfly and bumblebee communities (III). For each response variable, a set of nine competing models were built by including one to three of the following factors as explanatory variables: fallow type, the two landscape factors (forest and perennial grassland cover) and the two-way interactions among them. To capture spatial dependencies between sampling sites, a spatial Gaussian correlation structure was included in the models. The candidate models were compared using the Akaike Information Criterion, corrected for small sample sizes (AICc). Models with ΔAICc < 2 were considered equally good. In paper III, model averaging was performed over the best models to facilitate multi-model inference.

3.4.2 Ordination methods

Ordination methods were used to study the community composition of plants, butt erflies and bumblebees in fallows. Non-metric multidimensional scaling (NMDS) was employed in paper I to compare the plant composition among the four fallow types in the three study regions. In the Uusimaa region, fallow vegetation was also compared to that of cultivated grasslands, margins, and semi-natural meadows and pastures. Plant data on the semi-natural habitats were obtained from the national monitoring programme on the efficiency of the agri-environmental programme (MYTVAS), where similar field methods were used for the vegetation surveys. To test differences in plant species composition between the biotope types, the multi-response permutation procedure (MRPP) was applied. Based on the results of the NMDS, hierarchical clustering was performed using Ward's method.

In paper III, redundancy analysis (RDA) with Chord-transformed species data was performed to test the relationships between the species composition of flower-visiting insects and environmental variables. The environmental variables included local factors of fallow type and vegetation characteristics, and landscape factors of forest and grassland cover. Forward model selection by Monte Carlo permutation tests was conducted to identify the most important environmental variables explaining the species composition of butterflies and bumblebees.

Indicator species analysis (Dufrêne & Legendre 1997) was additionally employed to identify species associated with particular fallow or landscape types. Butterfly and bumblebee species with significant indicator values were reported in paper III. In this thesis, examples of indicator species are also shown for plants and birds.

4 RESULTS AND DISCUSSION

The two field studies produced novel information concerning the factors affecting the species diversity and community composition of multiple taxa in environmental fallows on boreal farmland. The vegetation survey, which encompassed four fallow types and three agricultural regions, provided a comprehensive overview on the habitat types developed under the Finnish environmental fallow scheme. The quasi-experiment was unique in simultaneously examining the impacts of fallow type and landscape structure on plants, butterflies, bumblebees and birds. The main results are summarized in Table 2. Examples of species associated with particular fallow and landscape types are provided in Table 3.

Table 2 Main results of papers I–III.

Paper	Main results
I	• Plant species richness and composition significantly differed between the four fallow types. • Highest plant species richness was observed on meadow fallows, while game fields had the lowest richness. • Grassland fallows were the most diverse fallow type in terms of vegetation diversity and composition, reflecting variation in age and management practices. • Vegetation of the annual fallow types was distinct from the perennial fallows and the other non-crop biotope types.
II	• Plant, butterfly, bumblebee and bird communities differed between fallow and landscape types. • Butterflies were most abundant in long-term grassland fallows and bumblebees in short-term meadow fallows. • Species richness of plants and butterflies was highest in landscapes with high forest cover. • Breeding birds of open farmland were most abundant in short-term meadow fallows in grassland-rich landscapes. • Foraging edge birds used short-term meadow fallows in open landscapes and long-term grassland fallows in forested landscapes.
III	• Species composition of butterflies and bumblebees was strongly related to forest cover in the surrounding landscape. • Mean niche breadth and dispersal capacity of butterfly and bumblebee communities were more related to fallow type and perennial grassland cover than to forest cover. • Butterfly species with narrow habitat breadth and poor dispersal capacity were relatively most abundant in long-term grassland fallows in landscapes rich in perennial grasslands. • Diet breadth of bumblebees was narrower in long-term grassland fallows than in short-term meadow fallows.

4.1 IMPACTS OF FALLOW TYPE AND LANDSCAPE ON THE DIVERSITY AND COMPOSITION OF ECOLOGICAL COMMUNITIES IN FALLOWS

4.1.1 Vascular plants

A total of 251 plant species were recorded in the two field studies. The most frequent species were *Elymus repens*, *Ranunculus repens* and *Phleum pratense*. Vascular plant species richness and composition significantly differed between the fallow types, reflecting differences in seed mixtures, management and fallow age (I). Species richness was highest in meadow fallows, which appeared to be due to the alternative seed mixtures containing low competitive grasses and meadow plants, and allowing for the establishment of numerous weeds from the seedbank. Grassland fallows established with common competitive grassland mixtures could also develop diverse swards when retained on the same field for several years. When three- to four-year-old meadow fallows and eight-year-old and older grassland fallows were compared, the plant species richness was equal at the two types (II). Temporal changes in plant species richness appear to be related to compositional changes from annual to perennial vegetation. As previously reported (Kovács-Hostyánszki et al. 2011, Steffan-Dewenter & Tscharntke 1997, Tscharntke et al. 2011), high species richness can be achieved in the early stages of succession when both annual and perennial species are present. A rapid decrease of annuals after the first years may lower the overall diversity, which could be seen in the meadow fallows. However, in long-term, plant species richness may increase with fallow age (Van Buskirk & Willi 2004).

Grassland fallows constituted the most heterogeneous fallow type in terms of plant species composition (I). The type includes grasslands that are kept in place for varying time periods ranging from two years to several decades, which have been established for different purposes, and are managed under various regimes. Some grassland fallows resembled production grasslands, while others had vegetation similar to semi-natural meadows. A few grassland and meadow fallows harboured plant species nationally classified as rare or endangered. These species were *Ajuga pyramidalis*, *Dianthus deltoides*, *Galium verum*, *Trifolium aureum* and *Trifolium spadiceum*. Meadow fallows and the annual fallow types formed more homogeneous groups than grassland fallows. Their vegetation was strongly affected by seed mixture and establishment success (Table 3). Game fields and landscape fields were dominated by annual vegetation, while meadow fallows were characterized by a combination of annuals and perennials.

Table 3 Species or species groupings associated with particular fallow or landscape types in the indicator species analysis (Dufrêne & Legendre 1997). The analysis identified more than ten plant species associated with each fallow type, but only species with the highest indicator values are shown. Sown plant species are marked in bold. Only plant data were collected from the game and landscape fields (I).

	Fallow type			
	Grassland fallow	Meadow fallow	Game field	Landscape field
Plants	*Anthriscus sylvestris*	***Leucanthemum vulgare***	***Cereals***	***Phacelia tanacetifolia***
	Achillea millefolium	***Festuca* sp.**	*Persicaria lapathifolia*	***Trifolium resupinatum***
	Lathyrus pratensis	*Taraxacum* sp.	***Brassica* sp.**	*Erysimum cheiranthoides*
	Angelica sylvestris	*Epilobium montanum*	***Pisum sativum***	*Chenopodium album*
	Filipendula ulmaria	*Cirsium arvense*	*Fallopia convolvulus*	*Stellaria media*
Bumblebees	*Bombus ruderarius*	*Bombus lucorum*	-	-
Butterflies	*Ochlodes sylvanus*		-	-
	Thymelicus lineola			
	Brenthis ino			
	Polyommatus semiargus			
Birds			-	-

Table 3 Continued

	Forest cover		Grassland cover	
	High forest cover	Low forest cover	High grassland cover	Low grassland cover
Plants	*Trifolium repens*			*Alchemilla* sp.
	Geranium sylvaticum			*Alnus incana*
	Achillea ptarmica			
	Carex sp.			
	Juncus sp.			
Bumblebees		*Bombus ruderarius*	*Bombus veteranus*	
		Bombus veteranus		
Butterflies		*Nymphalis urticae*		
		Coenonympha glycerion		
Birds	*Emberiza citrinella*		*Saxicola rubetra*	
			Alauda arvensis	

When compared to the other farmland biotopes (I), meadow fallows had species richness equal to semi-natural meadows, and even game fields harboured twice as many plant species as conventionally managed cereal fields (Salonen et al. 2011). Apart from the grassland type, the vegetation composition of fallows clearly differed from the other non-crop biotopes, thus creating landscape-wide diversity. These results support the idea that fallows help to maintain vegetation diversity on intensively cultivated farmland, although only a few fallows have plant communities of conservation interest (Boatman et al. 2011, Denys & Tscharntke 2002, Firbank et al. 2003, but see exception in Steffan-Dewenter & Tscharntke 1997).

Higher plant species richness was observed in the perennial fallows of forested rather than open landscapes (II) (Fig. 4), which was probably due to the enhanced colonization of fallows by species typical to forest edges. Furthermore, plant species richness in perennial fallow types was positively affected by field size, variation in sward height and fallow age (I). In contrast, dense and high vegetation structure and the high fertility level of a field were negatively related to species richness (I). Among the study regions, plant species richness was highest in Pirkanmaa, characterized by the most fine-grained landscapes, and lowest in the northernmost region Pohjois-Pohjanmaa (I). Two previous monitoring studies of semi-natural habitats on Finnish farmland have shown geographical location to explain the greatest part of the variation in plant species composition and diversity (Kivinen et al. 2006, Tarmi et al. 2009). These studies have found higher species richness in Southern and Eastern Finland compared to that in the northern and western parts of the country (Kivinen et al. 2006, Tarmi et al. 2009).

4.1.2 Butterflies and bumblebees

A total of 35 species and 2396 individuals of butterflies, and 14 species and 1458 individuals of bumblebees were recorded in the quasi-experiment. The most abundant butterfly species were *Aphantopus hyperantus*, *Thymelicus lineola* and *Ochlodes sylvanus*. Individuals of the *Bombus lucorum* group, *B. pascuorum* and *B. lapidarius* were the most abundant bumblebees.

Short-term meadow fallows and long-term grassland fallows supported different species assemblages of flower-visiting insects (II, III) (Fig. 4, Table 3). Meadow fallows, which provided more flowering plants than grassland fallows, attracted high numbers of bumblebees (II), although mainly of a few generalist species (III). This result is comparable with previous studies reporting that the occurrence of bumblebees is largely driven by the abundance and diversity of floral resources (Alanen et al. 2011, Kuussaari et al. 2011, Scheper et al. 2015). In contrast, butterflies were more abundant in grassland fallows, and their species richness was highest in grassland fallows of forested landscapes (II). Butterflies generally have lower dispersal capacity than bumblebees, and their occurrence is driven by the availability of larval food plants, along with nectar and pollen, which makes them more dependent on landscape complexity and long-term habitat management (Alanen et al. 2011, Kuussaari et al. 2011, Steffan-Dewenter & Tscharntke 1997). Forests may support butterflies by providing both shelter (Merckx et al. 2010), and adult and larval food (Öckinger et al. 2012a).

Long-term grassland fallows and landscapes with high cover of perennial grasslands best supported species with narrow niches and poor dispersal capacities (III) (Fig. 4): the mean habitat breadth of butterflies was narrowest in long-term grassland fallows in landscapes rich in perennial grasslands. The dispersal capacity of butterflies was also poorest in grassland-rich landscapes. The diet breadth of bumblebees was narrower in long-term grassland fallows than in short-term fallows. The positive impacts of perennial grasslands on specialist and sedentary butterflies are interesting, as they suggest that species vulnerable to environmental changes are not solely dependent on semi-natural habitats, but may also benefit from the occurrence of cultivated grasslands. However, the impacts of perennial grasslands can be both direct and indirect: grasslands may soften the arable matrix otherwise dominated by annual crops, thus facilitating dispersal among more suitable habitat patches. High perennial grassland cover may also indicate crop diversity or the occurrence of species-rich remnants of semi-natural grasslands in the landscape (Cousins 2006).

Forest cover in the surrounding landscape also affected the species composition of bumblebees and butterflies in perennial fallows, but the impacts on the relative abundance of species with narrow niches or low dispersal capacities were not as strong as those of perennial grasslands and fallow type (III). High forest cover in the study region (an average forest cover of 26% in “open” and 54% in “forested” landscapes) may partly explain the difference to the previous studies reporting the positive impacts of forest on specialist and less mobile lepidopteran species in semi-natural grasslands and field margins (Krämer et al. 2012, Merckx et al. 2010, Öckinger et al. 2012a). An increase in forest cover in forested landscapes may heighten the isolation of grassland habitat patches instead of increasing connectivity between them (Klaus et al. 2015, Ricketts et al. 2001). Along with landscape structure, species composition of butterflies was affected by the vegetation structure of a fallow: most species benefited from the high cover of bare ground, although a few species preferred dense swards (III).

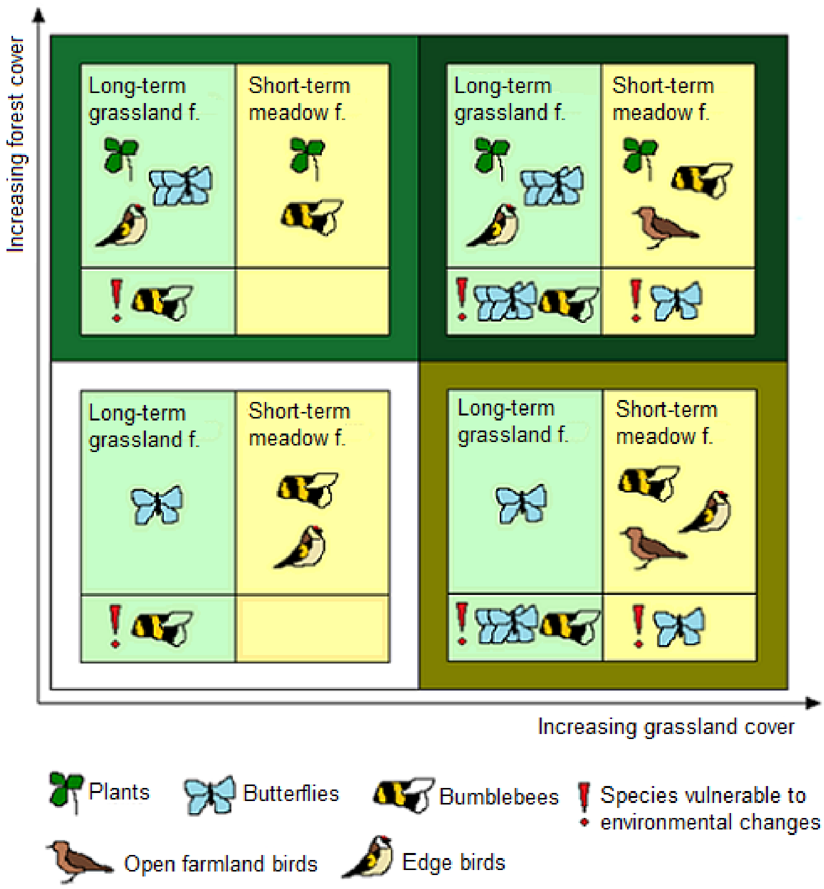

Figure 4 Responses of the studied species groups to two perennial fallow types and four landscape types. Species symbols indicate high species richness or abundance, or high relative abundance of species vulnerable to environmental changes (i.e. species with narrow niches or poor dispersal capacities). Double symbols denote that more than one of the measured biodiversity indicators for the species group had high values.

4.1.3 Birds

A total of 15 bird species, 200 territories and 181 foraging bird individuals were recorded in the quasi-experiment. Species with highest number of territories were *Sylvia communis* and *Saxicola rubetra*. *Carduelis carduelis* was the most abundant foraging edge bird in the fallows.

Many previous studies have highlighted the importance of short-term rotational fallows as breeding and feeding sites for farmland birds (Firbank et al. 2003, Henderson et al. 2000, Hyvönen & Huusela-Veistola 2011, Tscharntke et al. 2011). This study showed that both short-term meadow fallows and long-term grassland fallows can provide habitats for birds, but the suitability of the fallow types is strongly dependent on landscape context (II) (Fig. 4). Furthermore, the impacts were different for open farmland birds and edge species. The breeding density of open farmland birds was highest in the meadow fallows of landscapes rich in perennial grasslands. However, long-term grassland fallows supported more breeding pairs in landscapes with low perennial grassland cover. This may be interpreted as a "rare habitat effect": rare habitat types provide resources additional to those available in the landscape, and are thus of a particular importance to mobile species (Wretenberg et al. 2010). Foraging edge birds were most abundant in the meadow fallows of open landscapes, which may be due to the abundant seed food provided by arable weeds (II). In forested landscapes, long-term grassland fallows were used slightly more for foraging than meadow fallows. The results are noteworthy, as so far, no studies have examined the use of fallows for foraging in relation to landscape context.

4.2 PROMOTING DIFFERENT CONSERVATION OBJECTIVES THROUGH FALLOWS

My results show that fallows provide a flexible conservation tool that can be adjusted to serve different biodiversity objectives (Table 4). Conservation objectives on farmland are typically divided into the objectives addressing the intrinsic values of biodiversity and those focusing on functional biodiversity (Kleijn et al. 2011, Macfadyen et al. 2012, Smith et al. 2010). Within intrinsic biodiversity objectives, it may be useful to distinguish between the promotion of overall biodiversity and species of conservation concern, which may also require different conservation strategies (Korpela et al. 2013).

Intrinsic biodiversity values can best be enhanced by managing long-term fallows in complex landscapes (Fig. 4). For the promotion of species of conservation concern, long-term fallows in landscapes with high perennial grassland cover appears to be the best strategy, as these fallows supported flower-visiting insects with narrow niches and low dispersal capacities (III). Some old grassland fallows also generated meadow-type vegetation and harboured rare meadow plants (I, II). Though the management and restoration of traditional rural biotopes are the primary conservation tools for rare and endangered species in agricultural landscapes (Arponen et al. 2013, Krauss et al. 2010, Öckinger et al. 2010, Rassi et al. 2010), long-term fallows can complement the conservation strategy: as a less demanding and more widely available measure they can be implemented on a large scale to provide resources for species that are declining or vulnerable to future environmental changes. The benefits of long-term fallows were emphasized in landscapes rich in perennial grasslands. This is in line with previous studies suggesting that conservation initiatives targeted at species of conservation concern should focus on areas with low-intensity farming systems and complex landscapes (Kleijn et al. 2011, Smith et al. 2010).

High species diversity can be achieved in both short- and long-term fallows. The use of a diverse seed mixture is important especially in annual and short-term perennial fallows (I). In long-term fallows, the diversification of fallow vegetation can be supported by appropriate management such as extensive grazing, late-summer mowing and biomass removal, or scarification (Pykälä 2005, Pywell et al. 2007, Tarmi et al. 2011, Tilman & Isbell 2015). As regards to landscape positioning, establishing perennial fallows in less productive fields, often situated next to forests, appears reasonable not only on economic but also on ecological grounds (I, II). Placement is especially important for long-term fallows (II), since the colonization of new species from surrounding habitats diversifies species communities over the years.

However, the assessment of the biodiversity benefits of fallows should not be limited to the field scale, as many organisms respond to the environment at larger spatial scales (Benton et al. 2003, Gabriel et al. 2010). Although local alpha diversity is usually correlated with landscape-wide beta diversity, the latter has been reported to contribute more to overall biodiversity in agricultural landscapes (Clough et al. 2007, Flohre et al. 2011). Landscape heterogeneity can also buffer the effects of in-field management intensification to functional homogenization of communities (Gámez-Virués et al. 2015). From that point of view, the establishment and management of fallows should aim at creating habitat heterogeneity at the landscape scale (Benton et al. 2003). As many grassland fallows closely resemble production swards (I), they should be primarily established in landscapes with low perennial grassland cover. Along with the enhancement of biodiversity, grassland fallows in these landscapes may also provide other environmental and agronomic benefits: for example, they can diversify crop rotations, improve soil structure, and reduce erosion and nutrient leaching. Meadow fallows and annual fallow types form more distinct vegetation types than grassland fallows (I), and have thus the potential to enhance habitat heterogeneity in a wider array of landscapes. This conclusion is also supported by the result that, in landscapes with high grassland cover, the density of open farmland birds was higher in short-term meadow fallows than in grassland fallows, whereas the reverse was true in landscapes with low grassland cover (II). The strong impact of forest cover on the species composition of bumblebees and butterflies (III) suggests that the promotion of species diversity in these groups requires the establishment of fallows in both open and forested landscapes.

Table 4 Recommendations for the promotion of various species groups and conservation objectives through fallows.

Conservation objective	Fallow type and characteristics	Landscape positioning
Plants	Short-term fallows sown with diverse seed mixtures of species with low competitiveness, or long-term fallows (retention of old diverse grasslands); structurally heterogeneous swards	Low productivity fields in forested landscapes
Butterflies	Long-term fallows with diverse vegetation and abundant bare ground	Forested landscapes
Bumblebees	Short-term fallows sown with nectar and pollen plants	Any landscape
Open farmland birds	Short- or long-term fallows that are large enough for a bird territory or close to a suitable nesting habitat	Short-term meadow fallows in landscapes rich in perennial grasslands; in landscapes with low perennial grassland cover, long-term grassland fallows
Edge birds	Short- or long-term fallows	Short-term meadow fallows in open landscapes; long-term grassland fallows in forested landscapes
Species of conservation concern (butterflies and bumblebees)	Long-term fallows with diverse vegetation	Complex landscapes with high perennial grassland cover
Overall biodiversity at landscape or regional scale	All fallow types, various seed mixtures and management regimes	Landscape where a particular fallow type promotes habitat heterogeneity
Ecosystem services	Fallow type, establishment and management depending on the target ecosystem service	Intensively cultivated, simple landscapes

An important question regarding the intrinsic biodiversity value of fallows is which part of the species' responses to fallows results from population-level responses, and what is caused by behavioural responses (Kleijn et al. 2011). The present study cannot be used to infer population-level effects of fallowing – that would require monitoring in areas with and without fallows, preferably for several years. However, given the large area of fallows in Finland, population-level impacts are probable. Previous studies in Europe and North America have linked large-scale population trends of farmland birds to set-aside policies (Herkert 2009, Wretenberg et al. 2008). For insects, some indication of population-level effects was provided in a long-term fallow experiment in Finland, where lepidopteran species richness and abundance increased gradually over six years (Alanen et al. 2011).

Fallows can also be designed to promote ecosystem services by choosing seed mixture and management according to targeted organism preferences (Fiedler et al. 2008, Ramsden et al. 2015, Wratten et al. 2012). Ecosystem services were not directly studied in the present study. However, short-term meadow fallows attracted high numbers of bumblebees (II), which are important pollinators for many field crops (Goulson 2003, Kleijn et al. 2015). The fact that the observed bumblebees were mostly of a few generalist species does not necessarily reduce the fallows' value for pollination, as common generalist species contribute most to ecosystem services (Kleijn et al. 2011, 2015, Winfree et al. 2015). The abundance or even species richness of bumblebees were not dependent on the studied landscape features (II). This supports the idea that the promotion of ecosystem services should be focused on intensively cultivated areas, where the potential benefits of the enhanced services are largest (Kleijn et al. 2011).

4.3 LANDSCAPE MODERATION OF BIODIVERSITY EFFECTS

Although the importance of landscape context in moderating the biodiversity impacts of AES is well established (Batáry et al. 2011, Scheper et al. 2013, Tscharntke et al. 2005, 2012), there is a lack of empirical research that systematically examines which landscape characteristics are most important in determining the management effects on biodiversity (Tscharntke et al. 2012). When landscape context is included in studies, it is usually expressed as landscape complexity, defined simply as the total percentage of semi-natural habitats (Batáry et al. 2011, Scheper et al. 2013, Tscharntke et al. 2005, Winqvist et al. 2011). My results highlight two focal problems of this approach. First, forests strongly influence the diversity and composition of ecological farmland communities (II, III). However, the impacts of forests probably differ from those of open semi-natural habitats. Although the forest matrix and forest edges usually support insect and plant diversity on farmland (Kivinen et al. 2006, Krämer et al. 2012, Merckx et al. 2010, Öckinger et al. 2012b, Ma et al. 2013), forests may also constitute a barrier for low-dispersing species (Klaus et al. 2015, Öckinger et al. 2012b, Ricketts et al. 2001) and reduce the availability of more suitable grassland habitats. Understanding the specific role of forests is thus essential in areas with high forest cover.

Secondly, the impacts of perennial grasslands on the occurrence of farmland birds (II) and butterflies with narrow niches and poor dispersal capacities (III) proved that the evaluations of landscape-moderated effects of AES should not focus only on semi-natural habitats, but also consider the quality of arable matrix (Billeter et al. 2008, Scheper et al. 2013, Tscharntke et al. 2005). In Finland, perennial cultivated grasslands are the most common type of field use after spring cereals (Natural Resources Institute Finland 2015). Even intensively managed grasslands can provide suitable foraging resources, and nesting and overwintering sites for several taxa (Marini et al. 2012, Werling et al. 2014). Taking fallow fields into account is even more important – in the present study, meadow fallows supported vegetation diversity equal to semi-natural meadows (I). Besides providing habitats for wildlife, both fallows and cultivated grasslands may make an intensively cultivated agricultural matrix less hostile for dispersing species, thus promoting movement among highly fragmented semi-natural grasslands. In future studies assessing the landscape-moderated effects of AES, incorporating such potentially important land-use types, or a measure of land-use diversity, would be reasonable.

4.4 IMPLICATIONS FOR AGRI-ENVIRONMENTAL POLICY

Environmental fallows can significantly contribute to the biodiversity of intensively cultivated boreal landscapes. Environmental fallows in Finland currently cover 8% of all agricultural land, and are relatively evenly distributed in different agricultural regions of the country (Natural Resources Institute Finland 2015). The popularity of the scheme can be explained by fair compensation rates combined with poor profitability of agricultural production, along with the fact that fallows are easily implementable on any farm, as no special machinery or redesign of the cropping system are needed. The voluntariness of the scheme and high freedom in management regimes (use for fodder/pasture, mowing at any time) concurrently make the area and management of environmental fallows sensitive to changes in production environment such as agricultural commodity prices. Maintaining the established ecological network in the long-term is thus a challenge. Currently, the majority of environmental fallows in Finland are of the grassland type. Encouraging farmers to establish other fallow types, especially meadow fallows, would be beneficial for overall biodiversity. This could be done by adjusting compensation rates, promoting the availability of reasonably priced seed mixtures suitable to Finnish conditions and securing advisory support.

Large variation of grassland fallows in vegetation diversity and composition presents the question of the cost-efficiency of action-based fallow schemes. Like most AES, the Finnish environmental fallow scheme rewards farmers for specific management actions, although the same action can lead to different biodiversity outcomes depending on the environmental conditions and management histories. Results-oriented AES, which focuses on paying farmers for achieved biodiversity outcomes, could provide a more efficient way for biodiversity conservation through fallows (Hasund 2013, Matzdorf & Lorenz 2010). Results-oriented schemes would also encourage farmers to take their own initiative in developing the most optimal management regime for target species, thus promoting cultural and attitudinal change (Burton & Schwarz 2013, Schroeder et al. 2013). For the successful implementation of result-oriented schemes, it is crucial to develop effective biodiversity indicators that are measurable, identifiable and consistent with the scheme's goals along with securing sufficient advisory support for farmers (Burton & Schwarz 2013, Matzdorf et al. 2008, Schroeder et al. 2013).

Information from the present study can be utilized for the development of a results-oriented payment approach for farmland biodiversity management in Finland (Birge et al., in prep.). Based on my data, it is possible to compile a list of easily identifiable species associated with diverse plant and animal communities in fallows. These species could be used as indicators to determine the compensation rate for a fallow. Indicator species for grassland fallows might include the red-listed plant species registered in the vegetation surveys, along with the more common meadow plants such as *Fragaria vesca* and *Hypericum* species. Plants that provide resources for endangered animal species could also be included on the list. An example is *Valeriana sambucifolia*, the larval food plant of the endangered butterfly *Melitaea diamina* (Wahlberg 1998). The plant species was found in 4% of grassland fallows. However, as *V. sambucifolia* is difficult to differentiate from its close relative *V. officinalis*, classifying both plant species as indicators would be necessary.

My results also have implications for the ecological focus area requirement, introduced in the recent CAP reform as a part of 'greening', i.e. an attempt to promote environmental sustainability in agriculture (European Commission 2013). Since 2015, every farmer in the EU with more than 15 hectares of arable land is obliged to cover at least 5% of it by ecological focus areas such as fallows, nitrogen-fixing crops and landscape features. The measure includes exemptions for farms, which consist more than 75% of grasslands, along with regions with more than 50% of forest cover (this applies to most farms in Finland). On the basis of my results, these exemptions are without ecological grounds. Fallows in landscapes rich in perennial grasslands benefited butterfly species most vulnerable to environmental changes, whereas high forest cover supported the high species richness of butterflies and plants. Focusing fallows on the most intensively farmed areas with low forest and grassland cover is thus likely to reduce the intrinsic biodiversity values of fallowing, although it may be justified if the primary objective is to promote ecosystem services.

5 CONCLUSIONS AND FUTURE PERSPECTIVES

My thesis produced new information on utilizing environmental fallows to enhance different biodiversity objectives in varying landscapes. Species groups differed in their responses to fallow types and landscape. Furthermore, the impacts of a particular fallow type were modified by the landscape settings. Based on my results, I recommend a combination of the two main strategies to enhance the biodiversity benefits of fallowing:

- Highly dispersing generalist species particularly benefit from short-term fallows that are sown with diverse seed mixtures. These species contribute most to ecosystem services. The fast establishment of high plant diversity or vegetation that provides target organisms with specific plant resources, such as nectar and pollen or seed, is the main objective for the management of these fallows. The fallows should be primarily established in 1) intensively cultivated landscapes, where the potential benefits of the enhanced ecosystem services are largest, and 2) open landscapes rich in perennial grasslands, where they create larger ecological contrasts than grassland fallows, thus promoting overall diversity.
- Long-term fallows in landscapes with high forest and perennial grassland cover best promote intrinsic biodiversity values. These fallows support high species richness and may also harbour rare meadow plants and specialist insects with low dispersal capacity. The retention of already diverse old fallows should be the first priority. When new long-term fallows are established, they should be placed in less productive fields and complex landscapes.

Future AES evaluations should strive for more comprehensive understanding of what landscape features most affect the specific biodiversity objectives. Based on my results, I argue that the role of forest and perennial grasslands in driving the effectiveness of AES should be considered at least in areas where they are abundant. Furthermore, my results highlight the importance of including multiple species groups and conservation approaches in AES evaluation, to make realistic conclusions on the schemes' value for biodiversity. The impacts of AES, including fallows, on large-scale population trends of farmland species also deserve attention in future studies.

A relevant issue not covered in this study is the appropriate management of fallows. While management by cutting and biomass removal, or grazing usually positively impact the plant species diversity of grasslands (Pykälä 2005, Tarmi et al. 2011), it does not necessarily serve all organism groups. For example, mowing may adversely affect the density and diversity of grassland arthropods (Schmidt et al. 2008), and reduce the breeding success of ground-nesting birds (Vickery et al. 2001). Future studies should thus search for the best combinations of fallow type, landscape and management regime for the promotion of different species groups and biodiversity objectives. This would allow focusing management to sites that most benefit from it. Investigating new management methods would also be worthy of attention. For example, splitting fallows into strips that are mowed in different years or at varying heights would create variation in sward structure, thus enhancing the overall diversity within a fallow (Cizek et al. 2012, Schmidt et al. 2008). As meadow fallows proved, fallows do not need to resemble any existing or historical ecosystem in the area to contribute to biodiversity (Jackson & Hobbs 2009). Acknowledging the role of novel ecosystems does not diminish the importance of the simultaneous conservation of historical ecosystems, such as traditional rural biotopes, where still viable (Hobbs et al. 2014, Jackson & Hobbs 2009).

Along with biodiversity conservation, environmental fallows can provide a wide variety of other environmental benefits such as water protection or landscape amenity (Odgaard et al. 2013, Smith et al. 2008, Stoate et al. 2009). They can also be designed to provide agriculture with specific ecosystem services including pollination and biological pest control (Carvell et al. 2007, Fiedler et al. 2008, Ramsden et al. 2015, Wratten et al. 2012). However, this requires a lot of information on the impacts of seed mixture, management and environmental factors on the target and non-target organisms in fallows. Indiscriminate fallowing may not only be ineffective in producing environmental or agronomic benefits, but it can also cause damage to crops, e.g. by aggravating weed problems, which in turn may result in an increased use of herbicides. Currently, the potential of fallows is poorly exploited due to untargeted fallow schemes and lack of knowledge. As suggested before (Bommarco et al. 2013, Deguines et al. 2014, Doré et al. 2011, Tittonell 2014), future studies should address the question of how fallows could more effectively be integrated into agricultural production systems as a part of ecological intensification to help reduce dependency on anthropogenic inputs and stabilize yields while producing multiple environmental benefits.

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REFERENCES

Alanen, E.-L., Hyvönen, T., Lindgren, S., Härmä, O. et al. (2011) Differential responses of bumblebees and diurnal Lepidoptera to vegetation succession in long-term set-aside. Journal of Applied Ecology, 48, 1251–1259.

Arponen, A., Heikkinen, R.K., Paloniemi, R., Pöyry, J. et al. (2013) Improving conservation planning of semi-natural grasslands: integrating connectivity into agri-environment schemes. Biological Conservation, 160, 234–241.

Bäckman, J-P.C. & Tiainen, J. (2002) Habitat quality of field margins in a Finnish farmland area for bumblebees (Hymenoptera: Bombus and Psithyrus). Agriculture, Ecosystems and Environment, 89, 53–68.

Baessler, C. & Klotz, S. (2006) Effects of changes in agricultural land-use on landscape structure and arable weed vegetation over the last 50 years. Agriculture, Ecosystems and Environment, 115, 43–50.

Batáry, P., Báldi, A., Kleijn, D. & Tscharntke, T. (2011) Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. Proceedings of the Royal Society B, 278, 1894–1902.

Batáry, P., Dicks, L.V., Kleijn, D., & Sutherland, W.J. (2015) The role of agri-environment schemes in conservation and environmental management. Conservation Biology, 29, 1006–1016.

Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology and Evolution, 18, 182–188.

Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S.H. (1992) Bird census techniques. Academic Press, London.

Billeter, R., Liira, J., Bailey, D., Bugter, R. et al. (2008) Indicators for biodiversity in agricultural landscapes: a pan-European study. Journal of Applied Ecology, 45, 141–150.

Boatman, N.D., Jones, N.E., Conyers, S.T. & Pietravalle, S. (2011) Development of plant communities on set-aside in England. Agriculture, Ecosystems and Environment, 143, 8–19.

Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G. et al. (2010) Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. Proceedings of the Royal Society B, 277, 2075–2082.

Bommarco, R., Kleijn, D. & Potts, S.G. (2013) Ecological intensification: harnessing ecosystem services for food security. Trends in Ecology and Evolution, 28, 230–238.

Bühler, C. & Roth, T. (2011) Spread of common species results in local-scale floristic homogenization in grassland of Switzerland. Diversity and Distributions, 17, 1089–1098.

Bullock, J.M., Aronson, J., Newton, A.C., Pywell, R.F. et al. (2011) Restoration of ecosystem services and biodiversity: conflicts and opportunities. Trends in Ecology and Evolution, 26, 541–549.

Burton, R.J.F. & Schwarz, G. (2013) Result-oriented agri-environmental schemes in Europe and their potential for promoting behavioural change. Land Use Policy, 30, 628–641.

Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D. et al. (2007) Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. Journal of Applied Ecology, 44, 29–40.

Cizek, O., Zamecnik, J., Tropek, R., Kocarek, P. et al. (2012) Diversification of mowing regime increases arthropods diversity in species-poor cultural hay meadows. Journal of Insect Conservation, 16, 215–226.

Clough, Y., Holzschuh, A., Gabriel, D., Purtauf, T. et al. (2007). Alpha and beta diversity of arthropods and plants in organically and conventionally managed wheat fields. Journal of Applied Ecology, 44, 804–812.

Concepción, E.D., Díaz, M., Kleijn, D., Báldi, A. et al. (2012) Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. Journal of Applied Ecology, 49, 695–705.

Cousins, A. (2006) Plant species richness in midfield islets and road verges – The effect of landscape fragmentation. Biological Conservation, 127, 500–509.

Cousins, S.A.O., Ohlson, H. & Eriksson, O. (2007) Effects of historical and present fragmentation on plant species diversity in semi-natural grasslands in Swedish rural landscapes. Landscape Ecology, 22, 723–730.

Deguines, N., Jono, C., Baude, M., Henry, M. et al. (2014) Large-scale trade-off between agricultural intensification and crop pollination services. Frontiers in Ecology and the Environment, 12, 212–217.

Denys, C. & Tscharntke, T. (2002) Plant-insect communities and predator-prey ratios in field margin strips, adjacent crop fields, and fallows. Oecologia, 130, 315–324.

Díaz, S., Purvis, A., Cornelissen, J.H.C., Mace, G.M. et al. (2013) Functional traits, the phylogeny of function, and ecosystem service vulnerability. Ecology and Evolution, 3, 2958–2975.

Donald, P.F., Sanderson, F.J. Burfield, I.J. & van Bommel, F.P.J. (2006) Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. Agriculture, Ecosystems and Environment, 116, 189–196.

Doré, T., Makowski, D., Malézieux, E., Munier-Jolain, N. et al. (2011) Facing up to the paradigm of ecological intensification in agronomy: Revisiting methods, concepts and knowledge. European Journal of Agronomy, 34, 197–210.

Dufrêne, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs, 67, 345–366.

Eilers, E.J., Kremen, C., Greenleaf, S.S., Garber, A.K. et al. (2011) Contribution of Pollinator-Mediated Crops to Nutrients in the Human Food Supply. PLoS ONE, 6, e21363.

Ekroos, J., Heliölä, J. & Kuussaari, M. (2010). Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. Journal of Applied Ecology, 47, 459–467.

Eriksson O., Cousins S.A.O. & Bruun H.H. (2002) Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. Journal of Vegetation Science, 13, 743–748.

European Commission (2013) Overview of CAP Reform 2014–2020. Agricultural Policy Perspectives Brief No 5 / December 2013. http://ec.europa.eu/agriculture/policy-perspectives/policy-briefs/05_en.pdf. Last accessed: 24.4.2016.

Fiedler, A.K., Landis, D.A. & Wratten, S.D. (2008) Maximizing ecosystem services from conservation biological control: the role of habitat management. Biological Control, 45, 254–271.

Filippi-Codaccioni, O., Devictor, V., Bas, Y. & Julliard, R. (2010) Toward more concern for specialisation and less for species diversity in conserving farmland biodiversity. Biological Conservation, 143, 1493–1500.

Firbank, L.G., Smart, S.M., Crabb, J., Critchley, C.N.R. et al. (2003) Agronomic and ecological costs and benefits of set-aside in England. Agriculture, Ecosystems and Environment, 95, 73–85.

Flohre, A., Fischer, C., Aavik, T., Bengtsson, J. et al (2011) Agricultural intensification and biodiversity partitioning in European landscapes comparing plants, carabids, and birds. Ecological Applications, 21, 1772–81.

Frank, T., Aeschbacher, S., Barone, M., Künzle, I. et al. (2009) Beneficial arthropods respond differentially to wildflower areas of different age. Annales Zoologici Fennici, 46, 465–480.

Gabriel, D., Sait, S.M., Hodgson, J.A., Schmutz, U. et al. (2010) Scale matters: the impact of organic farming on biodiversity at different spatial scales. Ecology Letters, 13, 858–69.

Gámez-Virués, S., Perovic, D.J., Gossner, M.M., Börschig, C. et al. (2015) Landscape simplification filters species traits and drives biotic homogenization. Nature Communications, 6, 8568.

Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A. et al. (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science, 339, 1608–1611.

Goulson, D. (2003) Conserving wild bees for crop pollination. Food, Agriculture & Environment, 1, 142–144.

Greenleaf, S.S., Williams, N.M., Winfree, R. & Kremen, C. (2007) Bee foraging ranges and their relationship to body size. Oecologia, 153, 589–596.

Guerrero, I., Morales, M.B., Oñate, J.J., Geiger, F. et al. (2012) Response of ground-nesting farmland birds to agricultural intensification across Europe: Landscape and field level management factors. Biological Conservation, 152, 74–80.

Haaland, C., Naisbit, R.E. & Bersier, L. (2011) Sown wildflower strips for insect conservation: a review. Insect Conservation and Diversity, 4, 60–80.

Hansson, M. & Fogelfors, H. (1998) Management of permanent set-aside on arable land in Sweden. Journal of Applied Ecology, 35, 758-771.
Hasund, K.P. (2013) Indicator-based agri-environmental payments: A payment-by-result model for public goods with a Swedish application. Land Use Policy, 30, 223–233.
Henderson, I.G., Cooper, J., Fuller, R.J. & Vickery, J. (2000) The relative abundance of birds on set-aside and neighbouring fields in summer. Journal of Applied Ecology, 37, 335–347.
Hendrickx, F., Maelfait, J.P., Van Wingerden, W., Schweiger, O. et al. (2007) How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. Journal of Applied Ecology, 44, 340–351.
Herkert, J.R. (2009) Response of Bird Populations to Farmland Set-Aside Programs. Conservation Biology, 23, 1036–1040.
Hobbs, R.J., Higgs, E.S., Hall, C.M., Bridgewater, P. et al. (2014) Managing the whole landscape: historical, hybrid, and novel ecosystems. Frontiers in Ecology and the Environment, 12, 557–564.
Hyvönen, T. & Huusela-Veistola, E. (2011) Impact of seed mixture and mowing on food abundance for farmland birds in set-asides. Agriculture, Ecosystems and Environment, 143, 20–27.
Hyvönen, T., Ketoja, E., Salonen, J., Jalli, H. et al. (2003) Weed species diversity and community composition in organic and conventional cropping of spring cereals. Agriculture Ecosystems and Environment, 97, 131–149.
Jackson, S.T. & Hobbs, R.J. (2009) Ecological restoration in the light of ecological history. Science, 325, 567–569.
Keenleyside, C., Allen, B., Hart, K., Menadue, H. et al. (2011) Delivering environmental benefits through entry level agri-environment schemes in the EU. Report Prepared for DG Environment, Project ENV.B.1/ETU/2010/0035. Institute for European Environmental Policy, London.
Kivinen, S. (2005) Regional distribution and diversity perspectives of Finnish grasslands. Fennia, 183, 37–56.
Kivinen, S., Luoto, M., Kuussaari, M. & Helenius, J. (2006) Multi-species richness of boreal agricultural landscapes: effects of climate, biotope, soil and geographical location. Journal of Biogeography, 33, 862–875.
Klaus, F., Bass, J., Marholt, L., Müller, B. et al. (2015) Hedgerows have a barrier effect and channel pollinator movement in the agricultural landscape. Journal of Landscape Ecology, 8, 22–31.
Kleijn, D., Kohler, F., Báldi, A., Batáry, P. et al. (2009) On the relationship between farmland biodiversity and land-use intensity in Europe. Proceedings of the Royal Society B, 276, 903–909.
Kleijn, D., Rundlöf, M., Scheper, J., Smith, H. et al. (2011) Does conservation on farmland contribute to halting the biodiversity decline? Trends in Ecology and Evolution, 26, 474–481.
Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G. et al. (2015) Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. Nature Communications, 6, 7417.

Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I. et al. (2007) Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B, 274, 303–313.

Komonen, A., Grapputo, A., Kaitala, V., Kotiaho, J.S. et al. (2004) The role of niche breadth, resource availability and range position on the life history of butterflies. Oikos, 105, 41–54.

Korpela, E.L., Hyvönen, T., Lindgren, S. & Kuussaari, M. (2013) Can pollination services, species diversity and conservation be simultaneously promoted by sown wildflower strips on farmland? Agriculture, Ecosystems and Environment, 179, 18–24.

Kovács-Hostyánszki, A., Kőrösi, Á.,Orci, K.M., Batáry, P. et al. (2011) Set-aside promotes insect and plant diversity in a Central European country. Agriculture, Ecosystems and Environment, 141, 296–301.

Krämer, B., Poniatowski, D. & Fartmann, T. (2012) Effects of landscape and habitat quality on butterfly communities in pre-alpine calcareous grasslands. Biological Conservation, 152, 253-261.

Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K. et al. (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecology Letters, 13, 597–605.

Kuussaari, M., Heliölä, J., Luoto, M. & Pöyry, J. (2007) Determinants of local species richness of diurnal Lepidoptera in boreal agricultural landscapes. Agriculture, Ecosystems and Environment, 122, 366–376.

Kuussaari, M., Hyvönen, T. & Härmä, O. (2011) Pollinator insects benefit from rotational fallows. Agriculture, Ecosystems and Environment, 143, 28–36.

Kuussaari, M., Saarinen, M., Korpela, E.L., Pöyry, J. et al. (2014) Higher mobility of butterflies than moths connected to habitat suitability and body size in a release experiment. Ecology and Evolution, 4, 3800–3811.

Ma, M. & Herzon, I. (2014) Plant functional diversity in agricultural margins and fallow fields varies with landscape complexity level: Conservation implications. Journal for Nature Conservation, 22, 525–531.

Ma, M., Hietala, R., Kuussaari, M. & Helenius, J. 2013. Impacts of edge density of field patches on plant species richness and community turnover among margin habitats in agricultural landscapes. Ecological Indicators, 31, 25–34.

Macfadyen, S., Cunningham, S.A., Costamagna, A.C. & Schellhorn, N.A. (2012) Managing ecosystem services and biodiversity conservation in agricultural landscapes: are the solutions the same? Journal of Applied Ecology, 49, 690–694.

Marini, L., Quaranta, M., Fontana, P., Biesmeijer, J.C. et al. (2012) Landscape context and elevation affect pollinator communities in intensive apple orchards. Basic and Applied Ecology, 13, 681–689.

Marteinsdóttir, B. & Eriksson, O. (2014) Trait-based filtering from the regional species pool into local grassland communities. Journal of Plant Ecology, 7, 347–355.

Marttila, O., Haahtela, T., Aarnio, H. & Ojalainen, P. (1990) Suomen päiväperhoset (The Finnish butterflies). Kirjayhtymä, Helsinki, Finland.

Matzdorf, B., Kaiser, T. & Rohner, M.-S. (2008) Developing biodiversity indicator to design efficient agri-environmental schemes for extensively used grassland. Ecological Indicators, 8, 256–269.

Matzdorf, B. & Lorenz, J. (2010) How cost-effective are result-oriented agri-environmental measures?—An empirical analysis in Germany. Land Use Policy, 27, 535–544.

Merckx, T., Feber, R.E., Mclaughlan, C., Bourn, N.A. et al. (2010) Shelter benefits less mobile moth species: the field-scale effect of hedgerow trees. Agriculture, Ecosystems and Environment, 138, 147-151.

Natural Resources Institute Finland (2015) Utilized agricultural area 2015. http://stat.luke.fi/en/utilised-agricultural-area. Last accessed: 24.4.2016.

Öckinger, E., Bergman, K.-O., Franzén, M., Kadlec, T. et al. (2012a) The landscape matrix modifies the effect of habitat fragmentation in grassland butterflies. Landscape Ecology, 27, 121–131.

Öckinger, E., Lindborg, R., Sjödin, N.E. & Bommarco, R. (2012b) Landscape matrix modifies richness of plants and insects in grassland fragments. Ecography, 35, 259–267.

Öckinger, E., Schweiger, O., Crist, T.O., Debinski, D.M. et al. (2010) Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecology Letters, 13, 969–979.

Odgaard, M.V., Moeslund, J.E., Bøcher, P.K., Dalgaard, T. et al. (2013) The relative importance of geophysical constraints, amenity values, and farm-related factors in the dynamics of grassland set-aside. Agriculture, Ecosystems and Environment, 164, 286–291.

Pollard, E. & Yates, T. (1993) Monitoring butterflies for ecology and conservation. Chapman and Hall, London.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P. et al. (2010) Global pollinator declines: trends, impacts and drivers. Trends in Ecology and Evolution, 25, 345–353.

Power, A.G. (2010) Ecosystem services and agriculture: tradeoffs and synergies. Philosophical Transaction of the Royal Society B, 365, 2959–2971.

Pykälä, J. (2000) Mitigating human effects on European biodiversity through traditional animal husbandry. Conservation Biology, 14, 705–712.

Pykälä, J. (2005) Plant species responses to cattle grazing in mesic semi-natural grassland. Agriculture, Ecosystems and Environment, 108, 109–117.

Pywell, R.F., Bullock, J.M., Tallowin, J.B., Walker, K.J. et al. (2007) Enhancing diversity of species-poor grasslands: an experimental assessment of multiple constraints. Journal of Applied Ecology, 44, 81–94.

Pywell, R.F., Meek, W.R., Hulmes, L., Hulmes, S. et al. (2011) Management to enhance pollen and nectar resources for bumblebees and

butterflies within intensively farmed landscapes. Journal of Insect Conservation, 15, 853–864.
Ramsden, M.W., Menéndez, R., Leather, S.R. & Wäckers, F. (2015) Optimizing field margins for biocontrol services: The relative role of aphid abundance, annual floral resources, and overwinter habitat in enhancing aphid natural enemies. Agriculture, Ecosystems and Environment, 199, 94–104.
Rassi, P., Hyvärinen, E., Juslén, A., Mannerkoski, I. (Eds.) (2010) The 2010 Red List of Finnish Species. Ministry of the Environment and Finnish Environment Institute, Helsinki.
Ricketts, T.H. (2001) The matrix matters: effective isolation in fragmented landscapes. American Naturalist, 158, 87–99.
Salonen, J., Hyvönen, T. & Jalli, H. (2011) Composition of weed flora in spring cereals in Finland – a fourth survey. Agricultural and Food Science, 20, 245–261.
Scheper, J., Bommarco, R., Holzschuh, A., Potts, S.G. et al. (2015) Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. Journal of Applied Ecology, 52, 1165–1175.
Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G. et al. (2013) Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss – a meta-analysis. Ecology Letters, 16, 912–920.
Schmidt, M.H., Rocker, S., Hanafi, J. & Gigon, A. (2008) Rotational fallows as overwintering habitat for grassland arthropods: the case of spiders in fen meadows. Biodiversity Conservation, 17, 3003–3012.
Schroeder, L.A., Isselstein, J., Chaplin, S. & Peel, S. (2013) Agri-environment schemes: Farmers' acceptance and perception of potential 'Payment by Results' in grassland – A case study in England. Land Use Policy, 32, 134–144.
Smith, P., Martino, D., Cai, Z., Gwary, D. et al. (2008) Greenhouse gas mitigation in agriculture. Philosophical Transactions of the Royal Society B, 363, 789–813.
Smith, H.G., Öckinger, E. & Rundlöf, M. (2010) Biodiversity and the landscape ecology of agri-environment schemes. Aspects of Applied Biology, 100, 225–232.
Steffan-Dewenter, I. & Tscharntke, T. (2001) Succession of bee communities on fallows. Ecography, 24, 83–93.
Steffan-Dewenter, I. & Tscharntke, T. (1997) Early succession of butterfly and plant communities on set-aside fields. Oecologia, 109, 294–302.
Stoate, C., Baldi, A., Beja, P., Boatman, N. et al. (2009) Ecological impacts of early 21st century agricultural change in Europe – A review. Journal of Environmental Management, 91, 22–46.
Tarmi, S., Helenius, J. & Hyvönen, T. (2009) Importance of edaphic, spatial and management factors for plant communities of field boundaries. Agriculture, Ecosystems and Environment, 131, 201–206.

Tarmi, S., Helenius, J. & Hyvönen, T. (2011) The potential of cutting regimes to control problem weeds and enhance species diversity in an arable field margin buffer strip. Weed Research, 51, 641–649.

Tilman, D. & Isbell, F. (2015) Biodiversity: Recovery as nitrogen declines. Nature, 528, 336–337.

Tittonell, P. (2014) Ecological intensification of agriculture — sustainable by nature. Current Opinion in Environmental Sustainability, 8, 53–61.

Tscharntke, T., Batáry, P. & Dormann, C.F. (2011) Set-aside management: How do succession, sowing patterns and landscape context affect biodiversity? Agriculture, Ecosystems and Environment, 143, 37–44.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. et al. (2005) Landscape perspectives on agricultural intensification and biodiversity: ecosystem service management. Ecology Letters, 8, 857–874.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K. et al. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biological Reviews of the Cambridge Philosophical Society, 87, 661–85.

Van Buskirk J. & Willi Y. (2004) Enhancement of farmland biodiversity within set-aside land. Conservation Biology, 18, 987–994.

Vickery, J.A., Tallowin, J.R., Feber, R.E., Asteraki, E.J. et al. (2001) The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. Journal of Applied Ecology, 38, 647–664.

Wahlberg, N. (1998) Suomen uhanalaisia lajeja: tummaverkkoperhonen (*Melitaea diamina*). Suomen ympäristö 168. Suomen ympäristökeskus, Helsinki.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J. et al. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature, 414, 65–69.

Werling, B.P., Dickson, T.L., Isaacs, R., Gaines, H. et al. (2014) Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes. PNAS, 111, 1652–1657.

Whittingham, M.J. (2011) The future of agri-environment schemes: biodiversity gains and ecosystem service delivery? Journal of Applied Ecology, 48, 509–513.

Winfree, R., Fox, J.W., Williams, N.M., Reilly, J.R. et al. (2015) Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. Ecology Letters, 18, 626–635.

Winqvist, C., Bengtsson, J., Aavik, T., Berendse, F. et al. (2011) Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. Journal of Applied Ecology, 48, 570–579.

Wratten, S.D., Gillespie, M., Decourtye, A., Mader, E et al. (2012) Pollinator habitat enhancement: Benefits to other ecosystem services. Agriculture, Ecosystems and Environment, 159, 112–122.

Wretenberg, J., Lindström, Å., Svensson, S. & Part, T. (2007) Linking agricultural policies to population trends of Swedish farmland birds in different agricultural regions. Journal of Applied Ecology, 44, 933–941.

Wretenberg, J., Pärt, T. & Berg, Å. (2010) Changes in local species richness of farmland birds in relation to land-use changes and landscape structure. Biological Conservation, 143, 375–381.